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Separate Processing of Different Global-Motion Structures in Visual Cortex Is Revealed by fMRI

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Summary

The visual system has the remarkable ability to extract several types of meaningful global-motion signals, such as radial motion, translation motion, and rotation, for different visual functions and actions. In the monkey brain, different groups of cells in MST respond best to different types of global motion [1, 2], whereas in lower cortical areas including MT, no such differential responses have been found. Here, we show that an area (or areas) lower than MST in the human brain [3] responds to different types of global motion. A series of human functional magnetic resonance imaging (fMRI) experiments, in which attention was controlled for, indicated that the center of radial motion activates the corresponding location in the V3A representation, whereas translation motion activates mainly in a more peripheral representation of V3A. These results suggest that in the human brain, V3A is an area that differentially responds according to the type of global motion.

Results and Discussion

Monkey single-unit recording studies have revealed that global-motion patterns such as rotation, radial motion, and translation motion [4–7] are processed distinctly in MST [1, 2, 8]. What evidence exists for motion processing in human brains? In contrast to monkey brains, the results of several studies suggest that V3A in human brains is highly motion selective [9, 10]. V3A is regarded as an earlier stage of visual processing than MST [3]. Greater activation with coherent motion (velocities in a single general direction), as compared with random motion, was found in V3A but not in V1 [11–13]. However, how human V3A responds to different types of global motion has not been addressed. In the present paper, we show that human V3A differentially responds according to the type of global motion.

To measure global-motion activity in multiple areas, we presented human subjects with displays of radial motion, translation motion, and random motion. Radial motion is an important source of information for locomotion (e.g., heading) and can be either expansion or contraction. Translation motion is a pattern whose direction is perceived as the average of signals of randomly moving dots within a certain range of directions [14–17]. In the present study, we found that in human V3A, greater activity was associated with retinotopic locations corresponding to the focus of expansion (FOE) as compared to activity to random motion, whereas regions associated with more peripheral retinotopic regions were more activated with translation motion than random motion.

To assess activation based on global-motion type, we used a standard method of comparing MR activity to a specific global-motion type with activity to random motion. The stimuli consisted of limited-lifetime dots to ensure that the activity of units sensitive to local motion was statistically the same for global-motion stimuli and random-dot stimuli. Thus, if a difference in activity is found between a global type of motion and a random-motion pattern in some area, it would be regarded as a result of response to a pattern on a global scale [11, 12, 18, 19] rather than local motion.

In order to compare activity of different motion types, we systematically controlled for two confounding factors: opponent-motion suppression and attention. Opponent-motion suppression refers to activity of cells for neighboring opponent-motion direction signals [20, 21]. Opponent-motion suppression has been found in monkey MT [20] or human MT+ [21], but not in V1 for either species. This finding could make the brain respond differently to translation motion and random motion. For example, a translation motion in which dots move within ±45° from the spatiotemporal average has no dots moving in opposite directions, whereas in a random-motion display, two dots could move in opposite directions within a neighboring region. Thus, higher MT+ activity in the presence of translation motion as compared with random motion can be attributed to the lack of opponent motion in the global flow. To control for this factor, we used a *transparent*-translation-motion display in which half of the dots moved randomly within a 45° range and the other half within the opposite 45° range (e.g., 0° to 45° and 180° to 225°). As a result, two transparent-translation motions in opposite directions were perceived (Figures 1A and 1B). For this manipulation, the probability of local dots moving in opponent directions (within a local region) for the translation-motion display was statistically higher than in the random-motion display. The presence of a high degree of opponent motion, as compared to little or no opponent motion, results in lower MR activity. Thus, higher activity for transparent-translation motion as compared to random motion would be the result of the global flow pattern and not opponent suppression.

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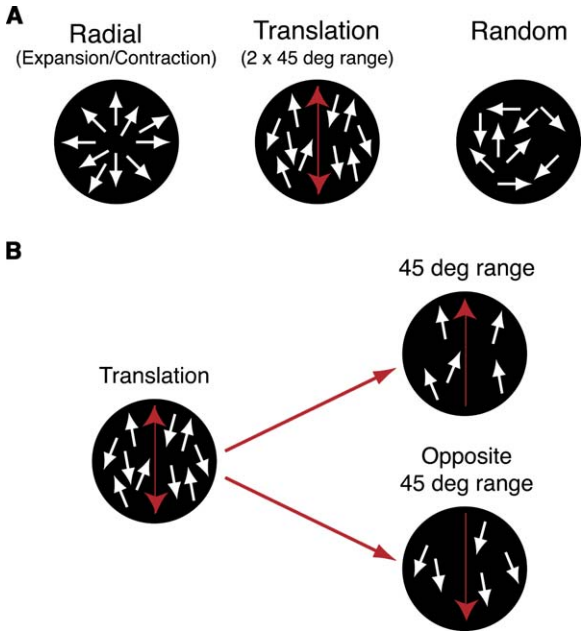

Figure 1. A Schematic Description of the Motion Stimuli

(A) The subjects viewed a radial-motion, translation-motion, or random-motion stimulus in 16 s epochs. The global-motion types were changed in a random order every 16 s.

(B) The translation-motion display consisted of two sets of global motion. In one set, the motion directions of the dots were limited to a 45° range, whereas in the other set, the motion directions of the dots were limited to the opposite 45° range. The two sets of global motion were perceived as transparent motion.

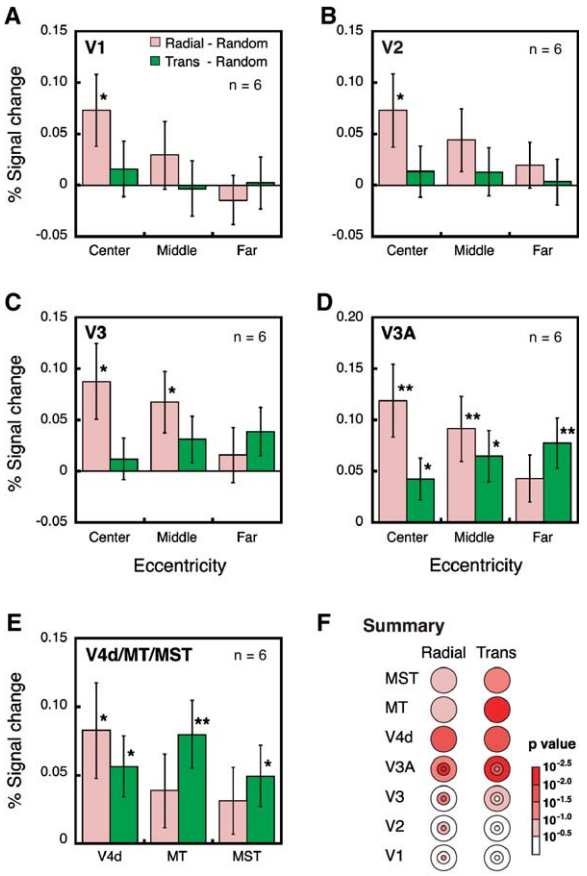

Figure 2. Mean MR Signal Amplitudes for Each Visual Area for Each Eccentricity

Each column represents the average of 24 data, i.e., 6 subjects × 4 time points. Error bars indicate the standard errors. The * sign indicates significant difference between radial motion (or translation motion) versus random motion ($p < 0.05$). The ** sign indicates $p < 0.01$. The red color scale in the summary (F) indicates p values from the paired t test for radial motion versus random motion (left column) and translation motion versus random motion (right column) for each visual area (V1, V2, V3, V3A, V4d, MT, and MST). Three concentric circles in V1, V2, V3, and V3A represent eccentricity (center < 2°, middle < 5°, and far > 5°) in those visual areas. Radial motion produced significantly stronger MR signals than random motion in the following visual areas: central V1 ($p < 0.05$), central V2 ($p = 0.052$), central and middle V3 ($p < 0.05$), central and middle V3A ($p < 0.05$), and V4d ($p < 0.05$). On the other hand, translation motion produced significantly stronger MR signals than random motion in central and middle V3A ($p < 0.05$), far V3A ($p < 0.01$), V4d ($p < 0.05$), MT ($p < 0.01$), and MST ($p < 0.05$).

As for attention, we asked subjects to perform a well-established task [22, 23] that was independent of the global-motion type. Each trial lasted for 4 s. During the first 1980 ms, a motion stimulus was presented. The subjects had to respond in the remaining 2020 ms. During the 1980 ms presentation, the speed of motion was different between the first and second intervals (both 990 ms) of a motion-stimulus presentation. Subjects were instructed to press a response key to indicate which of the two intervals had a greater speed. The same motion-speed discrimination task was given in all of the three motion types in order to ensure that subjects attended equally in all motion conditions [22, 23].

There were four trials in each epoch of 16 s. In each epoch, the same type of motion was presented: For transparent-translation motion, each of four pairs of direction ranges covering 90° in total was presented on each trial, so that 360° motion directions were covered in an epoch. For radial motion, in two trials, dots moved outward (expansion) from the center of the display, whereas in the other two trials, they moved inward (contraction). The presentation order of the four trials was randomized. For random motion, local dots moved within the 360° range for an entire epoch. The dot density was kept constant throughout the region in all the types of motion so that local-motion signals were equivalent. Within one scan, the same set of local-motion signals were presented for the three types of motion. We measured fMRI activity on a flattened occipital patch that indicated the retinotopical locations in V1, V2, V3 [24, 25], the locations of MT/MST [26], and other areas including V4d [27], V3B [28], and KO [29] as well as V3.

A larger amount of MR signal for the radial motion or translation motion, as compared to the random motion, can be regarded as activity related to the overall pattern of radial or translation motion. The activity patterns for these two types of motion were dramatically different in these low-level stages. Figures 2A–2E and Figure 3 indicate that the general tendency of activity for translation motion increased with increasing eccentricity in relatively higher stages such as V3 and V3A. On the other hand, activity for radial motion decreased with increasing eccentricity in V1, V2, V3, and V3A. A two-way ANOVA for motion type (radial versus random motion)

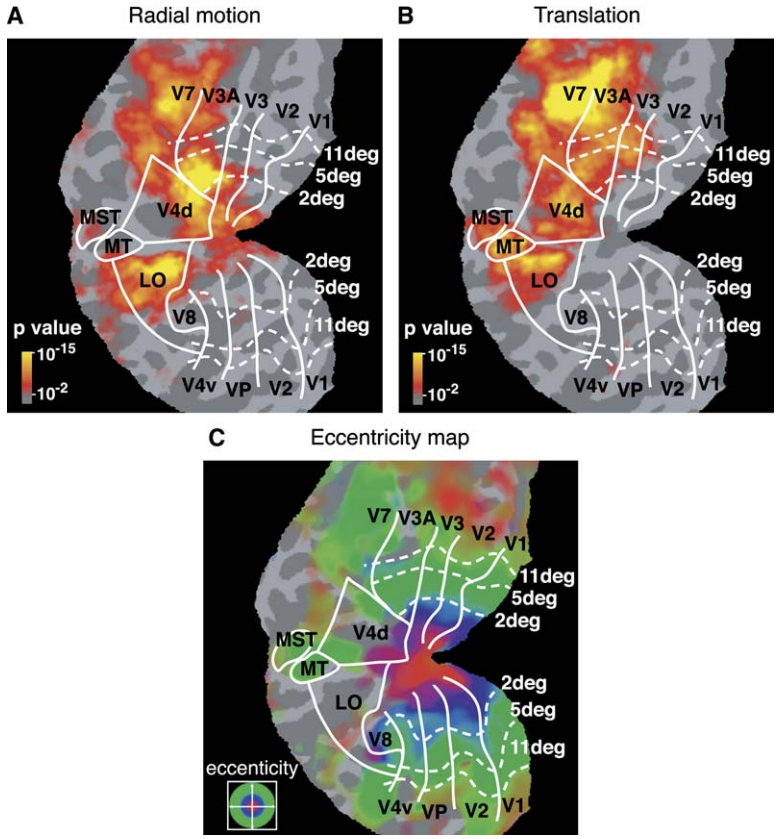

Figure 3. Activation Maps from the First Experiment

(A) Activation map for radial motion in a representative subject (left hemisphere). Average activation across six subjects was painted onto a flattened cortical map of a representative subject. For radial motion, activation was mostly seen in the central representation of V1 (<2°), V2 (<2°), V3 (<5°), and V3A (<5°).

(B) For translation motion, activation was seen in the peripheral V3 (>2°), V3A (>2°), and MT/MST.

(C) Eccentricity map of the representative subject obtained from a separate experiment. The red area in the image indicates voxels that responded maximally when the stimulus was presented in the fovea. The blue and green areas indicate voxels that responded maximally to the parafoveal and peripheral stimuli.

and eccentricity (center < 2°, middle < 5° versus periphery > 5°) was applied to V1, V2, V3, and V3A. A significant interaction between motion type and eccentricity was found in V1 ($p < 0.0001$), V2 ($p < 0.05$), V3 ($p < 0.01$), and V3A ($p < 0.0001$). The results of two-way ANOVA of motion type (translation versus random motion) and eccentricity showed that the interaction between motion type and eccentricity was significant in V3 ($p < 0.05$) and V3A ($p < 0.0001$).

These results were replicated in a control experiment (see Control 1 in the Experimental Procedures) in which the duration of the first and the second intervals varied randomly between 660 and 1320 ms (average duration was kept at 990 ms). This result excludes the possibility that the subjects paid attention to changes in motion speed, which could have been predicted to occur. In addition, because the probability of opponent local motion is higher with the transparent-translation-motion display than with the random-motion display, the higher activity with transparent-translation motion than with the random motion cannot be attributed to opponent suppression [20, 21].

In summary, the central representation of V1, V2, V3, and V3A was activated with radial motion, whereas the peripheral representation of V3A was activated with translation motion, suggesting that differential processing of global motion starts at least in V3A.

In the first experiment, FOE was presented at the center of the visual field. There are at least two possible explanations for the central representation in the low-level areas being more activated with radial motion. The central region of radial-motion stimuli has all directions of motion (all velocities point outward or inward in this region). In addition, the foveal representation in low-level visual areas has smaller receptive fields than more-peripheral representation. Thus, one possibility is that multiple populations of local directionally selective neurons may be excited particularly for the foveal representation because the central region of radial-motion stimuli contains all motion directions. The second possibility is that a specific pattern of radial motion around FOE drives a greater response.

To examine which possibility is plausible, we shifted the location of the FOE from the fixation point in a second experiment. If the activity is highest in the cortical location corresponding to FOE irrespective of whether FOE is presented in the central or peripheral visual field, then this finding would support the second possibility. In contrast, the first possibility does not predict this particular pattern of activity.

In the second experiment, we examined three conditions. In the first condition, FOE was presented at the fovea (the same location as in Experiment 1). In the second condition, FOE was shifted away by 4.5°. In the third condition, random motion was presented. The three conditions were alternated in a random order. The other aspects of the procedure were identical to the procedure used in Experiment 1.

As shown in Figure 4, when FOE was presented in the fovea, the pattern of results was very similar to the results for the radial-motion condition in Experiment 1. On the other hand, when FOE was presented in the 4.5° eccentricity (indicated as "the middle" in the figure), no particular signal enhancement was observed in V1,

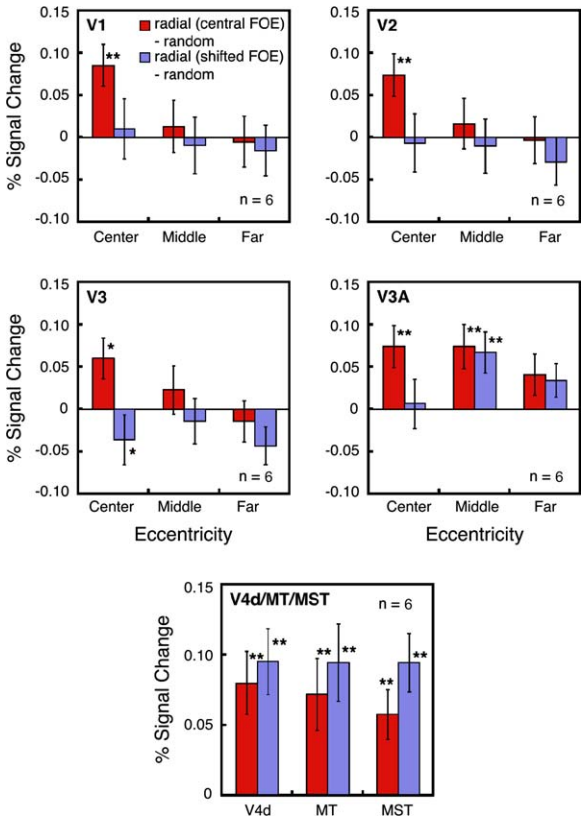

Figure 4. The Results from Experiment 2, in which Expansion and Contraction Were Superimposed

FOE was presented either in the fixation (red) or 4.5° away from the fixation (blue). For purposes of simplicity, we use the term FOE to refer to the focus of expansion as well as the focus of contraction. For the central FOE condition, radial motion produced significantly stronger MR signals than random motion in the following visual areas: central V1 ($p < 0.01$), central V2 ($p < 0.01$), central V3 ($p < 0.05$), central and middle V3A ($p < 0.01$), V4d ($p < 0.01$), MT ($p < 0.01$) and MST ($p < 0.01$). For the shifted FOE condition, on the other hand, radial motion produced significantly stronger MR signals than random motion only in the middle V3A ($p < 0.01$), V4d ($p < 0.01$), MT ($p < 0.01$), and MST ($p < 0.01$). Note that the strongest activity in V3A was observed in the middle representation when the FOE was presented at 4.5° eccentricity.

V2, and V3 as compared with the random-motion display. In V3A, however, only the representation corresponding to FOE (V3A middle) responded with a significantly greater signal to radial motion than to random motion ($p < 0.001$).

The results indicate that an excited location of V3A depends on the location of the FOE in the visual field. These results cannot be explained by the hypothesis that in Experiment 1 the foveal representation of V3A was excited because local units for multiple directions at the fovea were excited when radial motion was presented in the center. The results are consistent with the hypothesis that V3A responds most strongly to FOE, irrespective of where the FOE is presented in the visual field.

Two other issues might account for the present results. First, in the speed-discrimination task, the spatial distribution of attention may vary as a function of retinal location and motion type. Specifically, subjects might perform the task with greater attention to FOE in the central regions of the visual field for radial-motion display, whereas they might have greater attention to more-peripheral regions for global-flow motion display. A second concern is that in the main experiment, the direction of the translation motion switched among four alternatives every 4 s, whereas for the radial-motion pattern, the stimuli switched between two alternatives (expansion and contraction). This concern raises the possibility that adaptation effects had differential roles in the two types of motion displays.

To examine these issues, we conducted a third experiment with three conditions. In the first and second conditions, radial motion was presented with FOE at the fixation point and 4.5° shifted away from the fixation point, respectively. In the third condition, transparent-translation displays were used. For avoiding the possibility that subjects directed attention differently to the different types of motion, a control task was performed. During presentation of a motion display, for the first 500 ms in every 1 s, subjects (who had not participated in the previous experiments) were presented with a pale red dot in a location that was randomly chosen in each presentation or with nothing, and they were instructed to press a button depending on whether a dot was presented or not within the remaining 500 ms interval (see Experimental Procedures). This manipulation ensured that attention was not directed to any particular place [10, 30]. For avoiding adaptation effects, the direction of the translation motion was switched between two alternatives—similar to the radial-motion display. Thus, in each display, two opposite ranges of directions covering 90° were presented in an alternating pattern.

The results indicated two findings. First, the location of V3A that corresponds to FOE was significantly more activated with the radial-motion display than with random motion when the FOE was presented in the center ($p < 0.0001$) and at the 4.5° eccentricity location ($p < 0.001$). Second, the peripheral representation of V3A was more significantly activated with the translation-motion display than random motion ($p < 0.0001$). Thus these results rule out the aforementioned attention and adaptation issues.

A well-established view of motion processing in the monkey brain is that motion signals processed at low-level cortical areas, including V1, involve the recovery of local-motion signals regardless of the type of global motion; sensitivity to different motion patterns becomes different at higher extrastriate areas such as MST [1, 31, 32]. However, our fMRI results with humans are in accord with the hypothesis that in the human brain, differential processing for radial motion and translation motion occurs at V3A, which is lower than MST. V3A responds best to FOE irrespective of where it is presented in central or more-peripheral regions of the visual field. On the other hand, the peripheral representation in V3A responds best to translation motion.

Experimental Procedures

Subjects

The subjects ranged in age between 22 and 38 yr. All subjects (n = 6 in each experiment) had normal or corrected-to-normal vision. One of the subjects was an author, and the other subjects were naive with

regard to the purpose of the experiment. Informed consent was obtained from all subjects. The experiment was performed in compliance with relevant laws and the institutional guidelines of Massachusetts General Hospital (#2000P-001155).

Visual Stimulus

Visual stimuli were generated in real time on a Macintosh G4 computer outside the magnet bore. A color LCD projector (Sharp Note Vision 6; 1024 × 768 pixels, 75 Hz) was used to project the image onto a translucent projection screen located near the subject's head inside the bore. The subjects viewed the screen by looking up onto an adjustable mirror that was angled at about 45° to each subject's normal line of sight. The screen size was 27 × 20 cm. A fixation bull's-eye was presented at the center of the screen. The viewing distance (the distance between the display and the mirror and the distance between the mirror and the observer) was 55 cm. There were three types of motion: translation motion, radial, and random. For all motion types, 200 moving dots were presented in a circular aperture, 20.6° in diameter. In all three types of motion displays, the luminance of the dots and the background was 59.8 cd/m^2 and 0 cd/m^2, respectively. The dot density was roughly the same in any region of the display.

In the first experiment, for translation motion, the direction of motion of the dots was within two opponent ranges of 45°, i.e., ±22.5° from the mean direction. The mean direction pairs were (0° and 180°), (45° and 225°), (90° and 270°), and (135° and 315°). During one epoch of 16 s, the mean directions of dots switched every 4 s, so that 360° motion directions were covered in an epoch. For radial motion, dots moved outward (expansion) or inward (contraction). During one epoch of 16 s, the directions of dots (expansion or contraction) switched randomly every 4 s. The motion directions of the dots covered 360°. For random motion, each dot moved in a random direction within a 360° range. In the three motion displays, the dots traveled at two speeds (see Attentional-Control Task below). Dots traveled 0.4° from one frame to another at the 37.5 Hz frame rate (=15°/s) in the slower motion display; in the faster display, the speed increased by 6%–20%, depending on the subject's performance. The lifetime of each dot was 6 frames (=160 ms).

In the second experiment, FOE was presented either at the fovea, as in the previous experiment, or at 4.5° eccentricity. One hundred expanding dots and 100 contracting dots were superimposed, so that both motion-pattern directions were perceived at the same time simultaneously to equate with the global-motion display in the first experiment.

In the third experiment, transparent-translation motion (identical to those used in Experiment 1) and radial motion displays—one with the focus at the fovea and the other with the focus at the 4.5° eccentricity (identical to Experiment 2)—were used.

Experimental Design

One run consisted of four sets of three epochs in Experiments 1 and 2 and of four sets of four epochs in Experiment 3, and each epoch consisted of four trials of 4 s. In each epoch, a different type of motion was presented. Therefore, the duration of one run was 4 s × 4 trials × 3 epochs × 4 sets = 192 s in Experiments 1 and 2 and 4 s × 4 trials × 4 epochs × 4 sets = 256 s in Experiment 3. The order of the presentation of the three types of motion displays was randomized within a set, and the direction of translation motion and radial motion was randomized within an epoch. Twelve runs were conducted for each subject.

Attention-Control Task

Two well-established methods to control attention were used [22, 23]. On each trial of Experiments 1 and 2, the subject viewed the motion stimulus for 1980 ms. The speed of the dots changed in the middle of the trial, by 6%–20% depending on the subject's performance. The subject judged whether the dots moved faster in the first or second interval by responding with a key-press. The response was made within 2020 ms following the stimulus display. We also conducted a control experiment in which the duration of the first and the second intervals varied randomly between 660 and 1320 ms while the other parameters remained the same (Control 1). On each trial of Experiment 3, for the first 500 ms in every 1 s, a red stationary dot was presented or no such dot was presented. The subjects were asked to push a button depending on whether the dot was presented or not during the remaining 500 ms. Subjects' performance was maintained between 65% and 85% accuracy by adjusting the difference in dot speeds between the first and second intervals in Experiments 1 and 2, and by adjusting saturation of the red dot in Experiment 3, respectively.

Imaging Procedures

The subjects were scanned in a 3T scanner with EPI (Siemens 3T Allegra). MR images were acquired by using a custom-built, quadrature-based, semi-cylindrical surface coil, with voxels of 3.125 mm in-plane and 3 mm slice. Each slice was oriented perpendicular to the calcarine sulcus, covering all visual areas in the occipital lobe as well as parietal and temporal regions.

Data Analysis

The boundaries of each visual area for each subject were defined in a separate experiment with the standardized retinotopic-stimulus method based on the phase maps for eccentricity and polar angle [24, 25]. These objectively defined borders were available for visual areas V1 (superior and inferior), V2 (superior and inferior), V3/VP, V3A, V4d, and V4v. The locations of MT and MST were defined by the method developed by Huk et al. [26]. In the main experiment, the images from each subject were motion corrected and smoothed with a Gaussian filter of 6 mm FWHM, by using FreeSurfer (http://surfer.nmr.mgh.harvard.edu/). Time-course data for all voxels within a functionally defined ROI (regions of interest), such as V1-center, were averaged for each hemisphere for each subject. These data were normalized for each subject as percent signal change from the mean activation of all the voxels in the ROI. Normalized time-course data were averaged across subjects. Finally, normalized ROI data were selectively averaged by epochs for each subject and condition.

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